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THE

AMERICAN NATURALIST

VOL. XXVII. September, 1893. 321

THE PHILOSOPHY OF FLOWER SEASONS.[1]

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The researches of recent botany have more than once suggested the vague outlines of a truth that, though manifestly requiring investigation, has as yet received but little definite expression. It is:—the philosophy that underlies the association of certain groups and types of flowering plants with certain definite seasons of the year; the principles that will show how this association accords with the "eternal fitness of things."

The subject is of broadly interesting scope, but its treatment requires caution because of the variety of somewhat conflicting considerations involved. Obviously the aim cannot be to find any single absolute principle that will cover all cases, but rather to make some broad general observations that shall embrace all the diverse circumstances and at the same time express each with greatest definiteness. The field for investigation must be clearly presented and have its data determinable with certainty and completeness, and such can be found in the flora of the northern U. S., eastward from the Rockies. This has been more thoroughly studied than any other so large section of American flora, and is familiar to a large proportion of students.

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[1] Condensed for THE AMERICAN NATURALIST from a more extended thesis on the subject.

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Taking this, then, as the field, here is the problem presenting itself:—From March to November each month brings a new prospect in field and forest, an edition of flower-life distinctively its own; and each edition seems thoroughly to harmonize with its own peculiar season. Each offers characteristic features, and every careful observer can feel in this succession of differing forms a harmony into which any decided change would break discordantly. To bring this more forcibly to the mind, conceive for a moment the existing series somewhat transposed: imagine the prairies brilliant with Solidago and dotted with the purple Aster in early May; Trillium adorning the woodlands in September; the vivid Lilium superbum and the flaming Asclepias tuberosa in the April meadows; Hepatica and Sanguinaria in mid-July; and Epigæa in late autumn. Entirely aside from the element of novelty, such a picture would be bewilderingly inharmonious, and its features out of tune with their position by virtue simply of their character,—in this there would be an appreciable and evident lack of fitness. To say that the fall flowers are not the spring flowers, or those of summer are neither, merely because they have chosen at random this season or that is neither science nor common sense. The truth is forced upon us that the various groups of flowering plants are not scattered indiscriminately from one end of the seasons to the other, but are regulated by definite systematic principles; and that just as relations can be traced between physical geography and geographical distribution, or between plant-history and geological periods, so is there a connection between the relations of season to season and the relations of their respective floras.

In this inquiry we see constantly the impossibility of drawing sharp lines of demarkation between successive groups of conditions; and, as in classification systems, so in serially arranging successive floras, it is impossible to follow a linear order. Also, exceptional instances are many, and hence, to reach conclusions that are broadly true, *predominant* types must be considered, though the unusual cases may be in themselves manifestly significant. Only a broad sweep of data can bring out a general connection between the multiplicity of considerations. To this end it will be reasonable to consider the groups of flowering plants in the most strictly natural order of their evolutionary relationships, from the lowest up. That this evolutionary system is largely based on floral structure is suggestively apropos of our theme, but how far the intimacy of the connection may extend the further development of the discussion will reveal.

Passing to the outline of recorded observation we may discuss each condition of the problem as it arises. The three seasons considered have these limits:—spring; late March, April, May: summer; June, July, August: autumn; September and October. *All* statements *refer only* to the area about covered by Gray's Revised Manual: the U. S. north of Tennessee and eastward from west Kansas.

Of the two series of flowering plants, the Gymnospermæ and Angiospermæ modern botany concedes that the former, from their near approach to the higher Pteridopyta, represent the lower character of development, though the highly specialized Coniferæ may rise to a position nearly *parallel* to the highest Angiospermæ. The Coniferæ comprise all our indigenous Gymnospermæ;—and all flower in the spring from late March to earliest May, none in summer or autumn.

In the Angiospermæ, the Monocotyledons and Dicotyledons are two nearly parallel classes, the Monocotyls, though not transitional, representing, as a class, a lower character of development than the Dicotyls. Compare first the two classes in a general manner: The indigenous Dicotyls number much over twice the indigenous Monocotyls, and of the latter over half are in the great orders Cyperaceæ and Graminaceæ. And these orders demand special attention, for they together represent one of the most remarkable instances of high specialization in the whole census of plant-life. Apropos of this let us call to mind for further use the five characters of organic development which certain carefully systematic evolutiontsts!! have recognized:—*typical* forms, which present all the main characters of their group with fullest intensity; *generalized-normal* which have the normal characters somewhat poorly developed and defined; *specialized-normal*, which retain the normal structure but with evident one-sided development of it; *generalized-aberrant*, which depart from the normal but drift toward several or many outside relationships; and *specialized-aberrant*, which go off on a distinct individual line of their own. The Cyperaeæ and Graminaceæ are *specialized-aberrant* Monocotyls; and as they depart from the rest of the Monocotyls in structure, so, in the main, does their blooming season stand apart. Though extending from May, it culminates, particularly with the Graminaceæ, in the late summer and early fall, and stretches on into October. With reference to all other Monocotyls, note that by far the majority,—typical, normal, and *generalized-aberrant*,—confine their blooming season to spring, or early summer, or mid-summer, though fewer in the last. But in late summer and autumn occur only a few isolated cases. Indeed, even in the Glumaceæ excepted in the last statements, the great predominant genus of Cyperaceæ, the genus Carex, including much over half the order, belongs strictly to May. On the other hand, the Dicotyls, the higher Angiospermæ, are spread straight through the seasons, from March to November, represented by forms of all characters,—typical, normal, and aberrant. Thus, excluding Graminaceæ and several genera of Cyperaceæ, the Dicotyls may be said to constitute almost the entire flora of late summer and of autumn.

The Spadicifloræ and Liliifloræ form two fairly distinct subclasses of Monocotyls, closely parallel and somewhat interrelated. Though a debatable question, the imperfect and reduced flowers so general in the Spadicifloræ rather justify the conclusion that these are of the lower order of development. Moreover, throughout this subclass diclinism predominates, while the Liliifloræ are generally both hermaphrodite and complete and with well-developed perianth.

Normal and typical Spadicifloræ are the Araceæ. All these flower in May or June, except Symplocarpus. That its odorous scapes push out of the swamp mud in April is presumably a provision to insure cross-fertilization of the inconspicuous, though strong-scented, spadices before they are hidden by the subsequent growth of the huge rank foliage. Later, through the summer, flower the Typhaceæ, which, as *generalized-aberrant* Spadicifloræ, represent a rather more advanced degree of specialization than most Araceæ. Also in mid-summer come the remarkable little Lemnaceæ, usually considered a highly *specialized-aberrant* offshoot from Araceæ, though the connection is doubtful.

Among Liliifloræ the three apocarpal orders, Alismaceæ, Juncaginaceæ, and Naiadaceæ, form a remarkably aberrant group, of few species, but wide-spread, particularly Sagittaria and Alisma. All come in late summer, and some among the exceptional non-glumaceous Monocotyls of autumn. Potamogeton, in Naiadaceæ, numbers a good many species, and comes late; but note that the genus is one of the most peculiarly specialized.

All the Spadicifloræ and Apocarpal Liliifloræ are scarce a tenth of the remaining Monocotyls, the Syncarpal Liliifloræ. This division naturally subdivides into the Hypogynæ and Epigynæ, somewhat parallel and closely inter-related. In the light of our present knowledge of the morphology of the hypogynous and epigynous flower there can be no doubt that the Epigynæ here represent the higher order of development, although many Hypogynæ may rise to a more than equivalent degree of specialization,—precisely as the genus Felis is considered to represent a lower order of development but a higher degree of specialization than the anthropoid apes.

In the non-glumaceous Hypogynæ most prominent is the order Liliaceæ, in which are, pre-eminently, typical and normal forms. Among the normal, particularly the more generalized, the first bloom in late April,—notably, for instance, Erythronium, about the earliest of Monocotyls. Scarcely later come Trillium, Uvularia, Smilacina, Polygonatum, Maianthemum, and others. Other genera extend through May and early June, and a few, finally, belong to mid-summer. Certain of these last, as Allium and Smilax, are, though normal, markedly more specialized than the principal spring-flowering genera. But the mid-summer genus Lilium claims peculiar prominence as an ideally "*typical*" genus in all the term implies. *Lilium philadelphicum*, *L. catesbæi*, *L. canadense*, and *L. superbum* stand together in the July meadows as the type of their order and of the Hypogynæ. Their high order of development and their blooming season has a significant bearing on our problem. The aquatic Pontederiaceæ and the ephemeral Commelinaceæ, both few in species, and the odd genera Aletris and Xyris, are of mid-summer. With Smilax comes the nearly-related Dioscorea. Markedly conspicuous mid-summer Hypogynæ, rather intermediate between Liliaceæ and Cyperaceæ, are the widespread and aberrant, glumaceous types, Juncaceæ. But even these are less highly specialized than the two great orders Cyperaceæ and Graminaceæ, comprising over half of all our Monocotyls. The Graminaceæ are unquestionably the more highly specialized, and as distinctly *aberrant,* among Liliifloræ, as are the Lilia *typical.* Their period of greatest predominance extends from mid-July well into October. In Cyperaceæ it is curious that over half the order, the great genus Carex, attains full perfection in May; while the *type*-genus Cyperus belongs to August and September, most other genera to mid-summer, and a few to June. But mark especially: all the summer and fall Cyperaceæ, save a very few, are hermaphrodite, while Carex is entirely unisexual. The significance of this will come up later.

The review of Monocotyls closes with the Epigynous Liliifloræ, a small group compared with the Hypogynæ, but peculiarly interesting. Of the *generalized-normal* order Amaryllidaceæ we have only one wide-spread species, the little Hypoxis, of early summer. Iris comes in the spring and Sisyrinchium a little later, both rather specialized genera. Finally, the crowning glory of its class is the highly specialized order Orchidaceæ. Late in May come the earliest forms,—Orchis, Arethusa, and Corallorhiza. In early June:—Pogonia, Liparis, Calopogon, Listera, several green Habenarias, and the splendid genus Cypripedium. The succession of species in this genus is instructive:—Earliest, in late May, comes the little white *C. candidum;* a little later the low stemless type with its large complicated flower, *C. acaule;* still later the small-flowered but tall-growing *C. parviflorum;* later yet, the large cousin of the last, *C. pubescens;* and latest, late in June, most robust, vigorous, and conspicuous, the splendid *C. spectabile.* In late June and through July come other Pogonias and Corallorhizas; Microstylis, Goodyera, and one or two Spiranthes, and all the most beautiful Habenarias. Last, in September and October, singularly isolated from nearly all their kinsman, are several of the little Spiranthes,—why they come thus is a baffling question. Retrospectively we remark that of non-glumaceous Liliifloræ the two predominant orders are Liliaceæ and Orchidaceæ; that the first are largely normal and generalized, the second aberrant and specialized; and that the first predominate in the spring, the second in summer.

In the Dicotyls two quite distinct subclasses may be recognized: the one, the Diclinæ, is a very natural group, small but of great importance, embracing the closely related orders of trees and shrubs, Platanaceæ, Juglandaceæ, Cupuliferæ, and Salicaceæ; the other, vastly the larger, exhibits a broad, rather indefinite range of characters, and may be termed, in contra-distinction, the "Hermaphroditæ," because hermaphroditism, though by no means universal, predominates in it. The Diclinæ obviously approach the Coniferæ, among Gymnospermæ, in wood-structure and manner of growth, and in amentaceous diclinous inflorescence. Whence there is just reason to consider them, though wonderfully specialized, of a lower character of development than the Hermaphroditæ. Unisexual flowers, or the analogues of unisexual flowers, are the rule in Gymnospermæ and the higher Pteridophyta, and hence it reasonably follows that diclinous Angiospermæ are lower than hermaphrodite; and, further, diclinism in all Angiospermæ is either a perpetuation of the ancestral type or a reversion to it. In Diclinæ and in the Spadicifloral Monocotyls it is probably a perpetuation; in Carex, many Graminaceæ, and elsewhere among Angiospermæ, more likely reversion, retrogressive evolution. Note here the peculiar fact that in spring, from early March to June, blossom these diclinous groups:—all Coniferæ, the Araceæ, the great genus Carex, the Diclinæ, the Lauraceæ, several diclinous Ranunculaceæ, Urticaceæ, and many others; while in summer and fall come only:—a few Alismaceæ and Typhaceæ, many Graminaceæ, the Euphorbiaceæ, some Urticaceæ, and a few other isolated cases, but altogether a comparatively small number,—especially so because the Graminaceæ mentioned rarely have spikes entirely of unisexual flowers and hence do not strictly fit the case. The diclinism occurring in many Compositæ is not referred to, because it is not analogous to diclinism in other plants, and the Compositæ are relegated to a category of their own by their highly specialized inflorescence;—their diclinous "capitum" is functionally equivalent to a single perfect flower in other Angiosperms. The blossoming of so many trees, especially the Diclinæ, in earliest spring, before leaf-budding, must evidently have at least partial connection with anemophilous cross-fertilization.

The Hermaphroditæ (this term only signifying a *predominant* character) parts naturally into the Choripetalæ and Sympetalæ, nearly parallel and somewhat inter-related. The first includes the Incompletæ (so-called Apetalæ), which cannot be naturally made a separate division. It is conceded now that the Sympetalæ are higher than the Choripetalæ, though the divisions are not successive, save in that the first probably rose from some aberrant form of the second. There are three clear sub-divisions of the Choripetalæ, partly serial and partly parallel,—Hypogynæ (including so-called Discifloræ), Perigynæ, and Epigynæ. The Epigynæ are past question the highest, and the Perigynæ rather intermediate.

Earliest of the Hypogynæ are the Ranunculaceæ, peculiarly normal and typical and distinctively spring-flowering, extending from mid-April to early June. Hepatica, Anemonella, Caltha, Ranunculus, Aquilegia,—all synonymous with spring. Note that the more specialized forms, such as Aquilegia, Delphinium, Aconitum, etc., are the later, and some Clematis belongs to summer. With this early order come also our Magnoliaceæ and Berberidaceæ; late in May the Dicentra and Corydalis; through May and June the particularly natural and normal order Cruciferæ, more specialized, however, than Ranunculaceæ. In April comes that wonderfully symmetrical and typical form of the Papaveraceæ, the Sanguinaria. Remarkably aberrant in habit, but rather generalized in floral structure is the Sarracenia. It blossoms in latest May and early June. Among the earliest blossoms is the so abundant little normal type, Claytonia. Viola is a large, distinctive, and cosmopolitan genus, rather specialized-normal in character. Oddly enough it has species in bloom from April to October, some blossoming both spring and fall, besides producing cleistogamous flowers all summer. Yet even in so constantly present blossoms we easily recognize a period during which they reach by far their greatest abundance and perfection, viz.: May and June. Two unique orders belong to summer, Cistaceæ and Hypericaceæ, the second the later and remarkable particularly for its polyadelphous stamens. The incomplete flowered Urticaceæ belong mainly to summer, all save the group of spring-flowering shrubs and trees, Morus, Celtis, Planera, and Ulmus. All these are diclinous or polygamous, and Ulmus seems to possibly and probably connect its order with the Diclinæ,—like these it flowers in March and early April. Turning back to the near relatives of the Ranunculaceæ we find in mid-summer the aquatic genera Cabomba, Brasenia, Nymphæa, Nuphar, and Nelumbo, all *specialized-normal,* practicularly Nelumbo, the latest to flower. The so-called Discifloral Hypogynæ rank somewhat above such typical forms as the Ranunculaceæ and Cruciferæ, and among them stand several important summer orders:—Caryophyllaceæ; Malvaceæ; the strange Euphorbiaceæ of July, August, and September; and the Geraniaceæ, of which the aberrant Impatiens is latest. Anacardiaceæ belong to June. But the two tree-families, Tiliaceæ and Sapindaceæ come in spring and early June.

In the Perigynæ the preëminently normal and typical order is Rosaceæ, standing here as the Ranunculaceæ among Hypogynæ. Somewhat later than the latter order in starting the Rosaceæ reach perfection in late May and through June. At much the same time, but scattered along later into the summer, comes the less normal order Saxifragaceæ, of which the aberrant genus Parnassia, an odd little type, holds an isolated place in the late autumn flora. The distinctive order Leguminosæ, by far the most numerous of our Choripetalæ, flourishes throughout the summer and well into autumn. The aberrant Drosera is summer-flowering. Rhamnaceæ, and, particularly, the diclinous Lauraceæ, and the Hamamelidaceæ, belong to spring,—though Hamamelis, oddly enough, blooms in October.

As the typical Hypogynæ are characteristic of spring, so the several more important orders of Epigynæ belong peculiarly to summer and early fall:—the great order Onagraceæ, and the Lythraceæ; in late summer the strangely organized Passiflora; in hottest July our Cactaceæ, pushed up from the southwest; and in fullest sovereignty in July and August, though stretching from May to October, the widespread Umbelliferæ; the peculiar tropical Cucurbitaceæ from July to October; the more generalized Araliaceæ mainly in spring; and the shrubs and trees of the Cornaceæ also early. The anomalous Asarum and Aristolochia are scattered from May to July.

The Sympetalæ part naturally into the Hypogynæ, isocarpal and anisocarpal; and the Epigynæ. In Hypogynæ typical Isocarpæ, the more generalized group, are Ericaceæ, coming from earliest spring late into May and early June, and, at the same time, the Diapensiaceæ and Primulaceæ, the last rather later. Pyroleæ, in which there is a reversion to charipetalism, extend into July. Polemoniaceæ, somewhat transitional to the Anisocarpæ, bloom through May, June and July. In Anisocarpæ note:—the tree-order Oleaceæ, early flowering; the parasitic Orobanchaceæ, scattered from April to October; Catalpa and Bignonia in spring, and the brilliant *Tecoma radicans* in July; the Borraginaceæ, few in spring, reach perfection in summer; Convolvulaceæ and the unique Solanaceæ, from mid-summer into autumn; the aquatic Utriculariaceæ, entirely in summer; the great specialized orders Scrophulariaceæ and Labiatæ, throughout the seasons but in greatest predominance from mid-summer late into autumn; also then the Verbenaceæ. Apocynaceæ and the highly *specialized-aberrant* Asclepiadaceæ come in mid-summer. Characteristic of autumn are the Gentianaceæ, whose relation to the two last named orders gives them a high rank. A few species occur much earlier than the typical genus Gentiana.

Turn to the Epigynæ :—Caprifoliaceæ and Rubiaceæ, though scattered, predominate in summer; Campanulaceæ, particularly in late summer and in autumn,—the finest type *C. americana,* coming in September. Late in summer and in September, the Lobeliaceæ are in fullest perfection,—the splendid *Lobelia cardinalis* and *L. syphilitica* being late. And lastly, we meet the vast order Compositæ, undoubtedly nearly the highest of flowering plants. So numerous a group would naturally spread throughout the seasons, but mark :—it comes in all its glory late in August and straightway through the autumn, when we have, among many, those gorgeous genera, Solidago and Aster. Here the fact confronts us, that in the autumn the higher Sympetalæ hold sweeping predominance over the higher Choripetalæ.

Few data of any consequence have been omitted from this review, and the evolutionary system followed has been defined step by step because upon it the fabric of the argument mainly depends. The deductions are these :—*From early spring to late autumn there is a progression in the general character of the flower-groups, from the lower to the higher,—successive groups succeeding each other in time, parallel groups coming synchronously.* And the later in order may be *types* of a higher character of development, *or* they may be *specializations* of a group whose *normal* forms belonged to an earlier season. In their blooming season, *the more perfect succeed the more simple ; the aberrant, the normal ; the specialized, the generalized.* But with the general observation arise certain modifying conditions. The blooming period may sometimes vary from the general rule to better bring the flowers among the most favorable conditions for cross-fertilization,—in the case of anemophilous pollination before referred to ; or, even more obviously, in the case of entomophilous pollination, though here it is often doubtful whether the flower adapts itself to the insect's season or vice versa. Again, plants that are frontiersmen from the characteristic vegetation of a hotter clime may be expected in the hottest of the seasons,—e. g.: the Cactaceæ. There is an evident limitation of the flowering of our trees and shrubs to spring and earliest summer. This may largely be due to the excess of vital energy held stored up in woody trunks and branches,—and in Coniferæ in the evergreen foliage,—ready to burst forth with the first coming of warmth. Diclinism is most frequent in the spring months,—where this occurs in the lower groups of plants the case is covered by the general principle; but when diclinism obtains in highly specialized forms, as a result of retrogressive evolution, the problem becomes difficult,—the interesting question suggests itself: Does reversion in structure here revert the flowering period to an earlier season? As a case in point, recall the genus Carex. Again, there is a determining function in the character of the flower's habitat:—The spring flowers seek largely the protection of the woodlands; marsh-plants reach perfection mainly in latest spring and through the summer, though some, like Caltha, are early; the aquatics of ponds and river glory in the summer sun; and the flowers of meadow and prairie and thicket-margin luxuriate from mid-summer to the end of autumn. This last recalls the recent observations of Conway McMillan on "tension-line flora," and we note with interest that the highly organized tension-line flora gives us our later blossoms to a large extent. Further, every practical botanist knows that the herbaceous flora of summer, as a whole, shows a great advance in *vegetative* luxuriance over the corresponding flora of spring. But it does not follow that that of fall in turn advances, for vegetative luxuriance means primarily—heat. Yet the truth remains that this is not the fundamental criterion of plant aristocracy,—in the giant calamite of geologic ages flowed humbler blood than flows to-day in the dandelion of our backyard grass-plots. So each new factor that arises, far from weakening, but adds significance to the fundamental principle.

Here the question rises: Why should there be a correspondence between the course of the flower seasons and the system of floral evolution? Solve this, and the "philosophy of flower seasons" is an open riddle. But for the present it is only possible to indicate the direction in which the answer probably lies: The most simple and generalized forms, coming first in the course of floral evolution, have had the longest time in which to adapt themselves to existent climatic conditions;

and, reciprocally, climatic conditions have become more and more favorable to the rapid development of the said forms. So a floral type that ages ago would have reached its perfection only after a long continuance of favoring season, now may burst into the fulness of its maturity with the first warmth of spring. But as change succeeded change in the course of time, a maximum point would be reached, from which the conditions would become less and less favorable to the rapid development of types surviving from an earlier age. Then these would dwindle from the earth,—replaced, driven out, by those that had come into existence in a later age. Thus, in the ages to come, the early flowers of to-day will disappear; to be replaced by what are now our later flowers; whose place, in turn, will be filled by forms that are yet to be. All this is but a bare suggestion, yet in it may be, perchance, the spark of truth that will guide further observation to a more definite decision.

This very relation between flowers and seasons that the evolutionary floral system brings to light, may, in turn, modify somewhat that system, and so eradicate many seeming anomalies. And thus the added law may be better established by the perfecting of the fundamental one,—and vice versa. This consideration cannot be ignored.

In the light of all these facts and their regulating principles we can feel with fullest power that harmony of relations in the flora of each succeeding month,—a harmony to which even the casual observer cannot be insensible. The quarter of our country we have scanned is a wide sweep—coast-plain, hill-regions, mountains, and prairie; and if it offers so significant suggestions we can justly say, inductively, that there must be much here that is of far wider application. At least, there is full cause to believe that more extended research in this little-tested field of flower philosophy will be well repaid; and it may, further, open up an analogous field, yet unthought-of, in the realms of lower, flowerless, plant-life. The story told, we realize that its plot is simply another instance of the expression of universal law in that which rather seems a law unto itself.